FRONTAL CALCIFICATION AND ITS FUNCTION IN SOME CRETACEOUS AND RECENT CRIBRIMORPH AND OTHER CHEILOSTOME BRYOZOA

BY

GILBERT POWELL LARWOOD

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INTRODUCTION

In the course of a general systematic revision certain basic patterns become evident in the structure of the frontal walls of cribrimorph bryozoans. From membranimorph precursors the cribrimorphs evolved increasingly complex structures in the elaboration of both secondary and tertiary frontal walls. These changes may be traced from a phase of diversification in the Cenomanian into the late Cretaceous and Caenozoic. The structure of Recent cribrimorph frontal walls tends to resemble that of the less heavily calcified Cretaceous forms. The extensive tertiary frontal wall calcification of some later Cretaceous cribrimorphs may be interpreted as a feature relating to the whole zoarium. Less marked frontal calcification in some Recent non-cribrimorph cheilostome bryozoans may be similarly interpreted.

THE SECONDARY FRONTAL WALL

Early Upper Cretaceous cheilostome bryozoans include genera with marginal spines which arched over the chitinous frontal membrane (the primary frontal wall) but which were not fused along the mid-line of the zooecia (Text-fig. 1*b*). *Anaptopora* and *Anotopora* from the Cenomanian are examples of such genera (Lang, 1961; 1921). Morphologically such genera demonstrate the derivation of cribrimorph costate secondary frontal walls from a membraniporid condition (Text-fig. 1*a*) (Lang, 1921; Larwood, 1962). In the Cenomanian such genera as *Otopora* and *Calpidopora* show the early development of costae firmly fused in the mid-line of the zooecia (Text-fig. 1*c*). In *Otopora* the costae are continuous with no intercostal spaces (Text-fig. 1*e*) and the same structure may be developed in *Hybopora* and *Kankapora* and in the uniserial genus *Corymboporella*, but these Cenomanian genera are imperfectly known. *Calpidopora* represents the more general condition with prominent and undivided intercostal spaces (lacunae).

The frontal structure of *Ctenopora*, another Cenomanian genus, in which subjacent calcareous tissue fills the intercostal spaces, is not found in other Cretaceous cribrimorphs (Text-fig. 1*d*). The Recent bicellariellid genus *Petalostegus* (Text-fig. 2) may

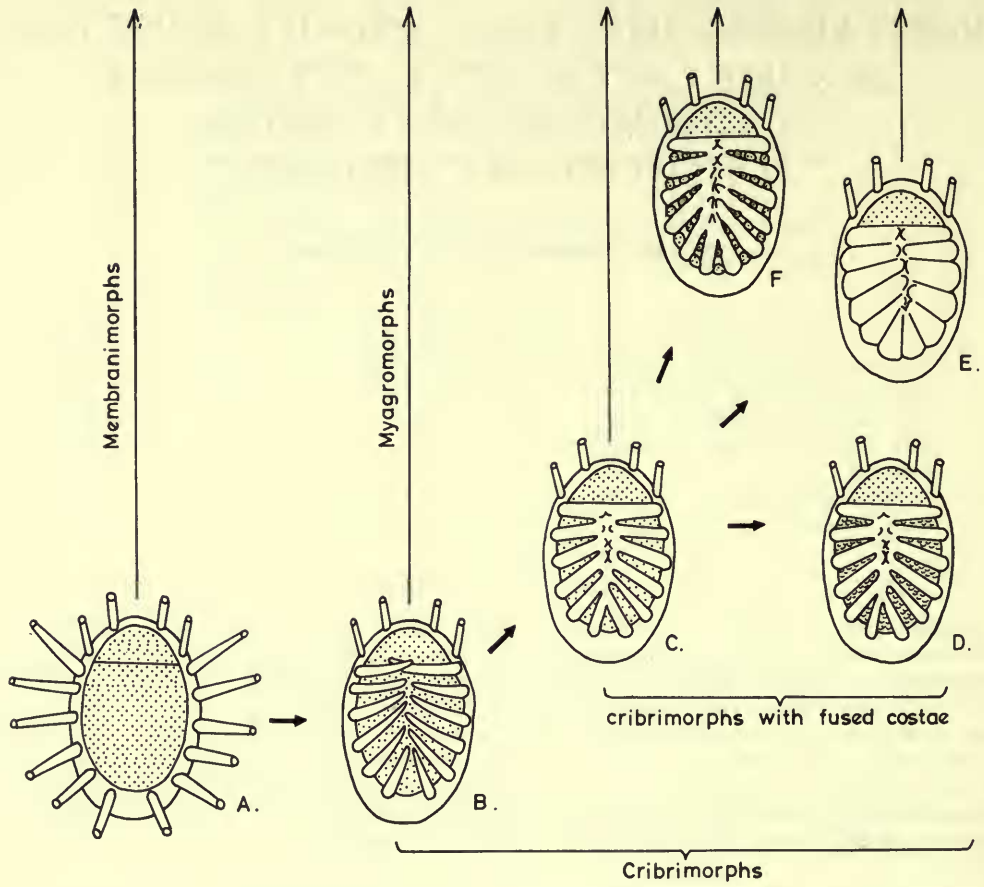

FIG. 1. Diagrams of single zooecia of a membranimorph and of derived early Cretaceous cribrimorphs to show variations in the structure of costate secondary frontal walls.

be cited as achieving a comparable secondary frontal wall of five flat plate-like spines with thickened edges and intervening pores. The porous thickened edges resemble irregular costae with pelmata (lumen pores) but their origin is clearly different from the costae connected by a subjacent lamina in *Ctenopora*.

Some Cenomanian cribrimorphs have divided intercostal spaces (Text-fig. 1*f*). *Polyceratopora euglypha* shows this condition but the precise nature of the lateral costal fusions is not clear. The Recent genus *Membraniporella* is most closely comparable to early Cretaceous cribrimorph genera of simple structure in which a few irregular lateral costal fusions are developed. *Membraniporella nitida* (Text-fig. 3) has these features but *M. marcusi* (Text-fig. 4) and *M. aragoi* (Text-fig. 5) demonstrate the formation of a costate secondary frontal wall from marginal spines which branch distally in one plane. In Cretaceous cribrimorphs the secondary frontal wall appears always to be formed by unbranched spines.

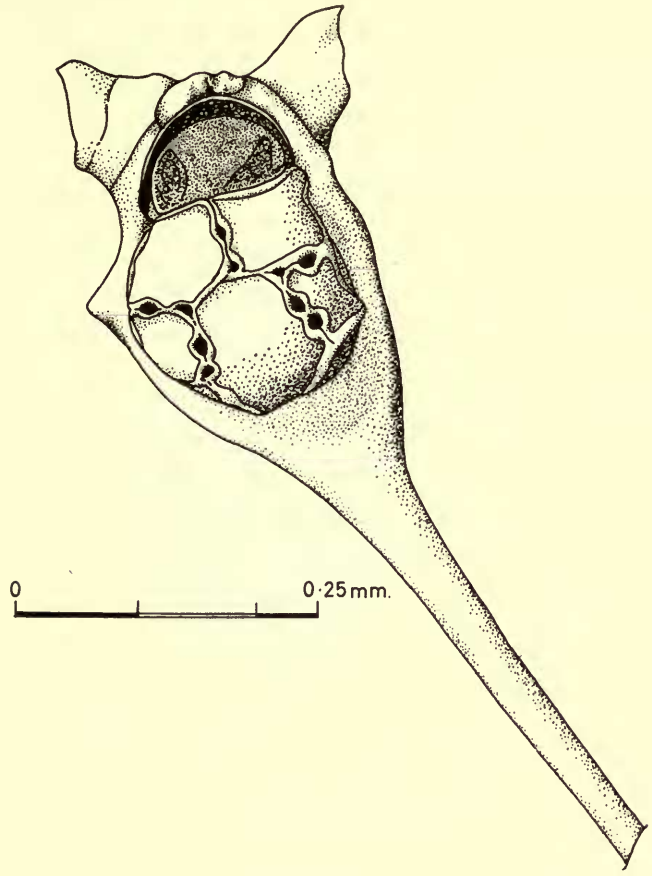

FIG. 2. *Petalostegus bicornis*. Recent. Single zooecium and paired distal-lateral avicularia. B.M.(N.H.) Zool. Dept. 99.7.1.3657.

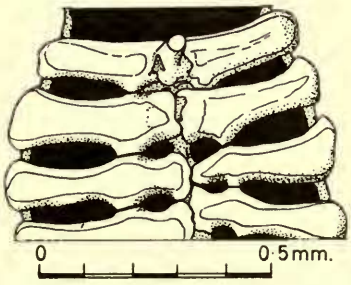

FIG. 3. *Membraniporella nitida* var. *intermedia*. Recent. Distal part of the costate secondary frontal wall of an adult zooecium. B.M.(N.H.) Zool. Dept. 08.3.23.2.

Only *Stichocados* among the Cretaceous genera assigned by Lang (1916, 1921) to the Cribrimorpha possesses minute branched spines on the secondary frontal wall. Current research by Mr. Håkansson, on extremely well preserved specimens of *Stichocados verruculosus* Marsson (1887) from the Danish Maastrichtian White Chalk, indicates that the secondary frontal wall in this genus lacks the hollow tapered costae characteristic of Cretaceous cribrimorphs. The secondary frontal wall is an expansion of calcareous tissue with rather regularly developed openings. Additional minute branched spines occur sparsely on the distal parts of the frontal wall and are most commonly developed adjacent to larger disto-lateral openings. The spines stand up at right angles to the surface of the frontal wall. I am not aware of similar structures occurring in true Cretaceous cribrimorphs and *Stichocados* should perhaps be referred to the Exechonellidae Harmer (1957 : 651) since the genus seems to have affinity with *Exechonella* Canu & Bassler (1927).

Another genus which possesses small branched spines on the secondary frontal wall is *Teuchopora* Neviani (1895). Harmer (1957, p. 896) has discussed this genus and Osburn (1940, p. 411) described a new species, *Teuchopora* (*Coleopora*) *americana*, which he placed in the Petraliidae. The species possesses thin, straight, distally branched spines on the secondary frontal wall (cf., B.M.(N.H.) Zool. Dept. specimen 1965.8.2.7). This example is most comparable with *Stichocados*.

Among post-Cenomanian Cretaceous cribrimorphs different species of *Pelmatopora* demonstrate the principal complications of the costate secondary frontal wall. Earlier species of *Pelmatopora* have undivided intercostal spaces (e.g., *P. solearis*, *P. d'orbignyi*). Such species as *P. fecampensis* and *P. pero* possess lateral costal fusions near the mid-line of the zooecium. *P. simplex*, *P. brydonei* and *P. gregoryi* are examples of species with costae joined by many lateral costal fusions. Larwood (1962) illustrates these species of *Pelmatopora*.

An additional, though by no means invariably developed, feature of cribrimorph costae is the presence of pores on the upper surface. These lumen pores are visible in some Recent cribrimorphs as small uncalcified areas which are occupied in life by soft tissue. Similar pores in the costae of fossil cribrimorphs may be termed pelmata and pelmatidia (large and small pores respectively). All species of *Pelmatopora* display pelmata or pelmatidia in the upper walls of the costae. In species with no lateral costal fusions a single pelma is commonly situated near the distal (inner) end of each costa. In species with a well developed series of lateral costal fusions a graded series of pelmata and pelmatidia occurs with the pelmata opposite each lateral costal fusion. In both fossil and Recent cribrimorphs pelmata and pelmatidia may be absent as in *Membraniporella nitidia* and *Cribrilaria radiata*. In some fossil genera pelmata and pelmatidia occur in some species of a genus but not in others. Compare, for example, *Leptocheilopora tenuilabrosa* with *L. vulnerata* (Larwood, 1962).

Among later Cretaceous cribrimorphs *Castanopora jurassica* exemplifies a marked development of pelmata, pelmatidia and lateral costal fusions (Larwood, 1962), and species of *Ubaghsia* such as *U. reticulata* and *U. ornata* demonstrate features developed by some heavily calcified forms in which there are very few pelmata on each costa and a small number of robust lateral costal fusions.

Although there are minor variations the basic pattern of this type of secondary

frontal wall is the same in Cretaceous and in many Recent cribrimorphs. The Recent species *Figularia figularis* has a single pelma at the proximal (outer) end of each costa and *Cribrilina punctata* has a series of nearly equal pelmatidia on each costa.

The structure of the costae in some other Recent cribrimorphs appears to be different. In *Gephyrotes nitido-punctata* prominent pelmata-like structures lie on the intercostal radii and the situation appears to be the same in *Puellina gattyae*. However, in both species small pores occur also above the median lumen of each costa and

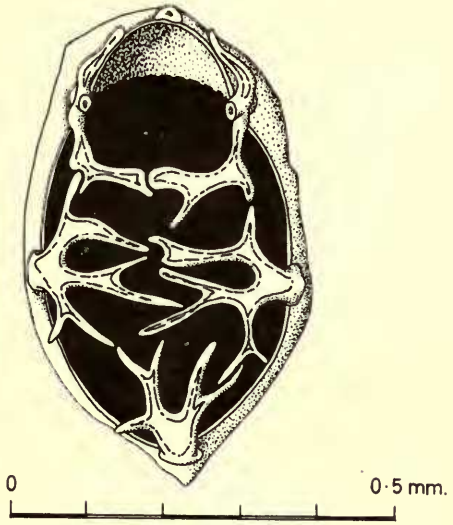

FIG. 4. *Membraniporella marcusi*. Recent. Single adult zooecium. B.M.(N.H.) Zool. Dept. LIX H.

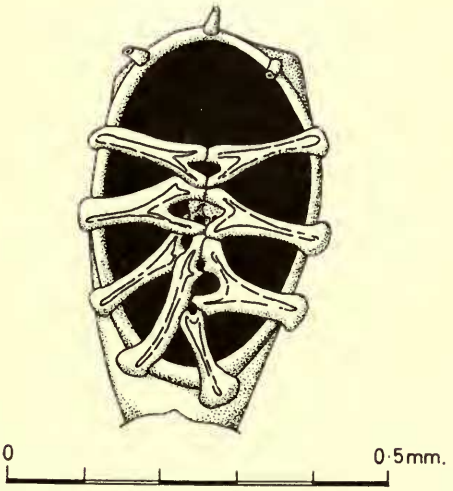

FIG. 5. *Membraniporella aragoi*. Recent. Single adult zooecium. B.M.(N.H.) Zool. Dept. 1965.8.6.2.

these may be interpreted as normal pelmatidia maintaining the same basic pattern of many other cribrimorphs.

Cribrilaria radiata (Text-fig. 6) has a distinctive and different frontal wall structure not seen in other Recent genera and, with the possible exception of *Corbulipora*, not known fossil. In *Cribrilaria* the costae rise steeply from the margins of the frontal wall forming a peripheral ring of near-vertical hollow spines. At the level of the secondary frontal wall each of these spines branches inward to form costae which lack pelmata or pelmatidia. McGillivray (1895) first described *Corbulipora* from the Middle Miocene of Victoria, Australia. The frontal wall of *Corbulipora* was described as being " ...raised, formed by a series of vertical ribs on each side, turning abruptly inwards and uniting to form a flat plate; ... ". I have not yet been able to examine specimens of this genus. McGillivray (1895) recognized three species (*C. ornata*, *C. cornuta* and *C. elevata*) and Maplestone (1901) described another species (*C. ampulla*) as having a " ...front much raised, with large margined pores, irregularly disposed on the surface; the sides with a regular series of upright elongate pores ". Brown (1958) described *C. pennata* with a " ...frontal shield flattened, consisting of a raised platform of spines projecting outwards laterally... '. I cannot envisage the precise nature of *Corbulipora* in relation to *Cribrilaria*, but it appears that the structure of the secondary frontal wall may be analogous in these genera.

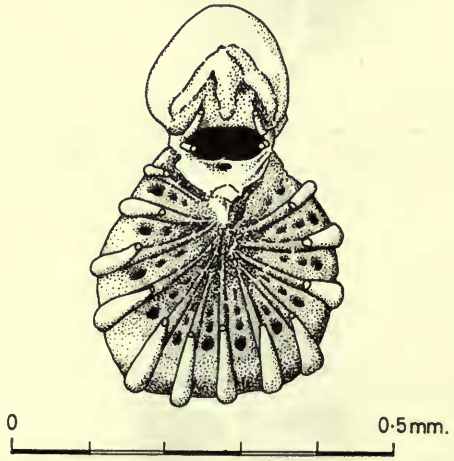

FIG. 6. *Cribrilaria radiata*. Recent. Single adult zooecium with hyperstomial ovicell. B.M.(N.H.) Zool. Dept. 99.5.1.720.

THE TERTIARY FRONTAL WALL

Numerous genera of later Cretaceous cribrimorphs develop a tertiary frontal wall of abundant calcareous tissue above the secondary costate frontal wall. Tertiary frontal walls are well displayed by *Tricephalopora*, *Phractoporella*, *Polycephalopora*, *Coelopora*, *Steginopora*, *Disteginopora* and *Ubaghsia*. In these, and in other genera, there is a general development of calcareous tissue which fills the interzooecial furrows covering the proximal gymnocyst of zooecia and often expanding onto the proximal and lateral

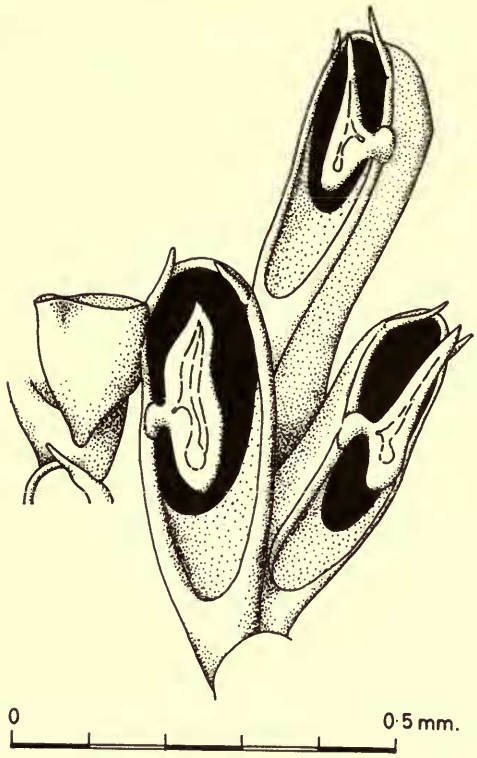

FIG. 7. *Canda clypeata*. Recent. Adult zooecia and an associated avicularium. B.M.(N.H.) Zool. Dept. 28.9.13.113.

areas of the costate secondary frontal walls. There is general upgrowth of the circum-oral tissue commonly incorporating avicularia and proximal and distal oral shields which result from the enlargement and fusion of distal and lateral oral spines with the enlarged apertural bars. In such genera as *Ubaghsia* this extra calcification forms an irregular robust and raised lattice of calcareous tissue above the general level of the zooecial secondary frontal walls. The extensive development of such tertiary frontal walls has no close parallel in Recent cribrimorph genera. Extensive olocystal or tremocystal skeletal thickening is achieved by some ascophoran bryozoans such as *Porina, Semihaswellia, Tremotoichos* and *Bathystomella*. The scale of this extra calcification is comparable with that of the tertiary frontal walls of some later Cretaceous cribrimorphs but its mode of formation is different.

THE FUNCTION OF EXTRA FRONTAL CALCIFICATION

Variation and complexity of costate secondary frontal walls in Cretaceous cribrimorphs relates to the activity and function of individual zooecia, but elaborate subsequent calcification to form a tertiary frontal wall poses a problem of interpretation. It is difficult to understand how the formation of a robust outer layer of calcareous tissue can be related to polypide activity. The mode of secretion of

tertiary frontal walls, or even of lesser amounts of interzooecial tissue, is obscure and information is lacking on the relations of the calcareous skeleton to the secretory soft tissues in Recent bryozoans. However, some " mantle-like " extension of secretory soft tissue over the whole colony seems to be indicated by the tertiary frontal wall structures which were developed by many Cretaceous cribrimorphs.

Functionally, the significance of a well developed tertiary frontal wall would seem to relate to the colony as a whole rather than directly to individual zooecia. Its development affords protection for the more delicate subjacent costate frontal walls of zooecia and for their contained polypides. It acts as a coarse outer filter to the zoarium precluding penetration by larger organisms or by coarse detritus and it may even be effective in retaining a certain amount of graded detritus forming a further protection over the surface of the zoarium.

A similar interpretation could be made of frontal structures of some much less calcified Cheilostomata. The single lateral scute-like spines of *Canda clypeata* (Text-fig. 7) clearly relate to the individual zooecia which bear them, but in multiserial laminar zoaria the frontal spines of adjoining zooecia form in effect a continuous lattice over the whole zoarium and their function relates also to the colony as a whole. Recent species of *Hiantopora—H. ferox* (Text-fig. 8) and *H. intermedia* (Text-figs. 9, 10)—demonstrate the overgrowth of branched marginal spines in association with prominent avicularia combining to form a frontal shield over each zooecium. Since these shields are developed by adjacent zooecia they form a protective barrier for the whole colony and a filter in which the largest openings are located over the orifices of the zooecia. Other structures may also function in this fashion, for example, the abundant and very prominent branched oral spines of such Recent species as *Chaperia cervicornis*.

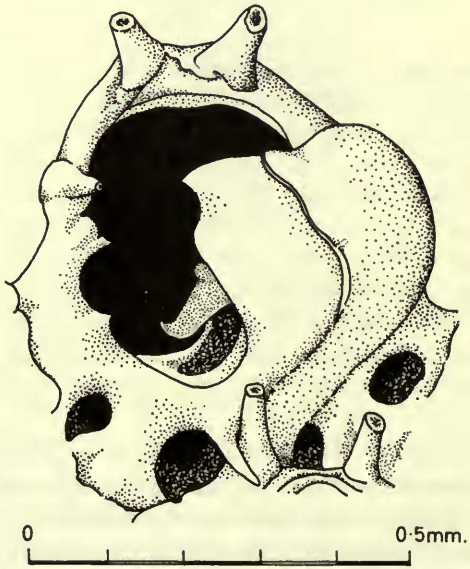

FIG. 8. *Hiantopora ferox*. Recent. Single adult zooecium with lateral avicularium. B.M.(N.H.) Zool. Dept. 99.7.1.1371.

The Cretaceous species *Stichocados verruculosus* Marsson has similarly well developed large and robust oral spines and it is significant that the minute branched spines rising from the secondary frontal wall are sited adjacent to the largest openings in that structure.

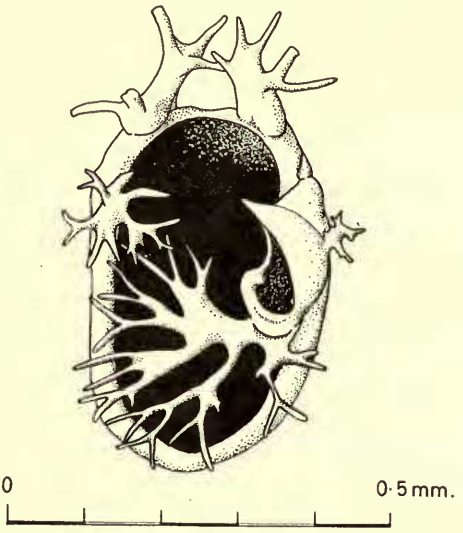

FIG. 9. *Hiantopora intermedia*. Recent. Single adult zooecium and an associated lateral avicularium. B.M.(N.H.) Zool. Dept. 28.3.6.52.

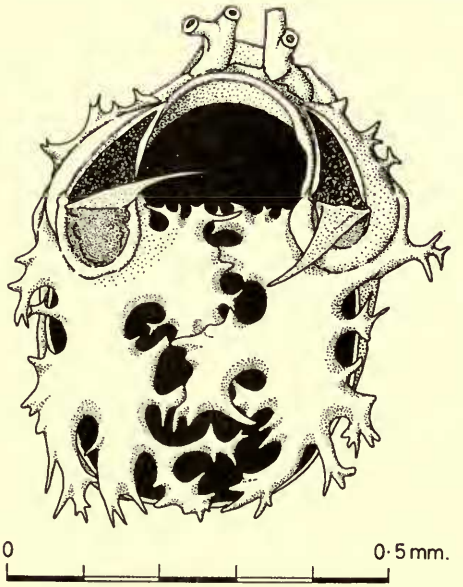

FIG. 10. *Hiantopora intermedia*. Recent. Single adult zooecium and paired oral avicularia. Note the robust development of frontal spines compared with those of the zooecium shown in Text-fig. 9. B.M.(N.H.) Zool. Dept. 28.9.13.22.

The complex tertiary frontal walls developed in Cretaceous cribrimorphs are a specialized example of a zoarial filter and protective lattice. Structures which are developed in relation to zooecial orifices and the variety of heterozooecia in the Cretaceous cribrimorphs are often incorporated into the secondary and tertiary frontal wall systems and will be considered elsewhere.

SUMMARY

The structure of the secondary frontal walls in some Cretaceous cribrimorphs is compared with that developed in the frontal walls of some Recent cribrimorphs. Cretaceous cribrimorph genera which develop tertiary frontal walls are considered and the function of extra frontal calcification generally is briefly discussed.

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I wish to thank particularly Miss P. L. Cook for much helpful advice and discussion, and the Keepers of the Departments of Zoology and Palaeontology at the British Museum (Natural History) for the loan of specimens. I also thank Mr. E. Håkansson, Mineralogisk Museum, Copenhagen, for the opportunity to examine and discuss the Maastrichtian species of *Stichocados*.

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G. P. Larwood, B.Sc., Ph.D. (Lond.), M.A. (Cantab.)
Department of Geology
Science Laboratories
University of Durham